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Author(s): Peter M. Narins
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Seismic Communication in Anuran Amphibians

White-lipped frogs thump the ground as they chirp

Peter M. Narins

Seismic communication is the exchange of information using self-generated vibrational signals transmitted via a substrate such as the soil, a plant stem, or even a blade of grass. This communication style affords many advantages for terrestrial animals. By understanding the advantages and limitations of this modality, one may more fully appreciate the selective pressures operating both on the organisms that employ seismic signals and on communication systems as a whole.

Seismic communication can take place without light, during day or night. Vibrational signals are most effective over a short range and have only short persistence. Thus they are well-suited for information exchange between nearby conspecifics; there is little danger of detection by distant predators.

Due to their comparatively long wavelengths, seismic signals are affected relatively little by obstacles in the soil. This feature of vibrational signals accounts for one of their potential drawbacks: the emitter may be difficult to locate, because phase differences between points on the body surface of a small receiver, such as a frog, would be minimal. Furthermore, there are clear mechanical limits on the upper frequency of seismic signal production, with the result that vertebrate vibratory signals are restricted to frequencies below several hundred Hz, the upper frequency for synchronous contraction of skeletal muscle. In this article, I concentrate on the terrestrial medium and do not consider the aquatic biotope; several excellent reviews address communication via aquatic surface waves (e.g., Bleckmann 1985, Markl 1983).

Sensitivity to substrate vibrations

It has long been known that many terrestrial animals are sensitive to low-level substrate vibrations. These animals include the cockroach Periplaneta (Autrum and Schneider 1948), a wide variety of insects (Markl 1983, Schwartzkopff 1974), snakes (Hartline 1971), and salamanders (Ross and Smith 1978, 1979, 1980). More recently, a comparable sensitivity was demonstrated in anuran amphibians (frogs and toads).

An example of an anuran species with a particularly acute vibrational sensitivity observable both behaviorally and neurophysiologically is the white-lipped frog, Leptodactylus albilabris. This ground-dwelling, nocturnally active amphibian is found in marshes and ditches and along mountain streams throughout much of the island of Puerto Rico (Rivero 1978). Males prefer vocalizing from within clumps of dense grass on the ground, often covered by fallen vegetation, or from shallow depressions or burrows in the muddy substrate. Relatively isolated individuals separated by several meters are common, although males are also frequently found calling in high densities around water-filled ditches. Females of this species are cryptically colored and silent; they are thought to move great distances during their nocturnal foraging, perhaps to acoustically sample males in the area (Drewry 1970).

If one approaches an isolated calling male white-lipped frog in its natural habitat, it almost immediately ceases to call. In fact, even on a moonless night the lightest footfall or finger tapping at distances of up to five meters from a single calling male will often cause that male to become silent for five or ten minutes. This remarkable behavior suggests that these animals might be detecting the presence of intruders (human or otherwise) by sensing the vibrations transmitted in the substrate. Similar sensitivity has been reported by Christensen-Dalsgaard and Jorgensen (1988) from studies of the European grassfrog, Rana temporaria, and by Elefandt (1982) studying Xenopus. These workers speculate that both species may use their seismic sense to detect water surface waves to localize conspecifics in the breeding ponds.
The physics of seismic waves

There are two basic classes of elastic waves that can propagate in a solid object such as the earth: body waves and surface waves. Body waves travel through the earth and are either of the high-velocity compressional (P) type or the low-velocity shear (S) type. Velocities through granite, for example, of 5.5 km/s and 3.0 km/s are typical for P-waves and S-waves, respectively. Moreover, because these waves are being dissipated within the earth, the major source of amplitude attenuation is via spherical spreading, just as for sound waves in free space. The amplitude of a compressional or shear wave falls off as \(1/r\) where \(r\) is the distance from the source.

The second basic class of elastic waves consists of those propagated disturbances restricted in their motion to the boundary layer at the earth's surface. Two types of well-studied surface waves are Love waves and Rayleigh waves, which differ both in their plane of polarization and their velocity. The plane of polarization of a seismic wave is that plane containing the particle motion, and the direction (or axis) of propagation is the direction of energy flow for the wave. Displacements of the substrate particles in Love waves are perpendicular to, and in Rayleigh waves parallel to, the vertical plane containing the axis of wave propagation. Love waves cause particle displacement to occur in a direction transverse to the axis of energy flow. In contrast, Rayleigh waves result in no transverse vibration, but they cause individual substrate particles to undergo a retrograde elliptical orbit, meaning that when the particle is at the top of its ellipse it is moving opposite to the direction of wave propagation.

Figure 1 shows the transverse (to the axis of propagation) motion of the substrate during a Love wave and the elliptical particle motion, restricted to the vertical plane, during a Rayleigh wave. Some variation in these ideal polarization patterns occurs due to both local inhomogeneities in the substrate and proximity to the source. Surface waves dissipate their energy in an ever-expanding circular pattern concentric with the source; as a result, the amplitude of a Rayleigh or Love wave decreases as \(1/r^{1/2}\), where \(r\) is the distance from the source. Thus, far from the source, the major remaining component of the seismic disturbance is the surface wave. Rayleigh waves propagate significantly slower than body waves; typical Rayleigh wave velocities in moist soil are 100 m/s (Lewis and

Figure 2. Experimental set-up used in the field to simultaneously measure the acoustic and seismic components of the call. The three geophones are oriented orthogonally, i.e., with their sensitive axes parallel to a line to the frog, horizontal and perpendicular to a line to the frog, and vertical. Each geophone output is recorded on a separate channel of the Teac cassette recorder. The animal's call is recorded on one channel of the Stellavox recorder, and the acoustic stimuli delivered from the Sony cassette player is simultaneously recorded on the second channel of the Stellavox and the Teac cassette recorders.
Narins 1985) and, in loose sand, 40–50 m/s (Brownell 1977). (For a more thorough treatment of seismic wave propagation see Richter 1958 or Bolt 1988.)

Measurement of seismic signals

Seismic vibrations in the earth, whether caused by an earth tremor or by an animal communicating with its neighbor, may be conveniently measured using the seismologists’ geophone. This device consists of a housing containing an internal coil held by a spring, which centers the coil in a strong magnetic field. The interaction of the coil mass and the spring stiffness creates a resonance at a frequency, f₀, below the range of interest. Above f₀, the open-circuit output voltage is proportional to the velocity of the housing (White 1983).

A geophone is designed to record substrate vibrations in a single plane of polarization. Thus, using an orthogonal array of three geophones, one may record wave motion in three planes simultaneously (e.g., longitudinal horizontal, transverse horizontal, and vertical; Figure 2). When we attached the appropriate amplifiers and headphones to a geophone array placed in the vicinity of a calling white-lipped frog, we were quite surprised to hear that, concomitant with the call, this animal produces an audible thump readily detected by the geophones (Figure 3). The vertically polarized geophone consistently produced the largest response amplitude, which at a distance of 1 m is approximately 2 cm/s² peak acceleration (Lewis and Narins 1985). In all cases, the geophones oriented in the horizontal plane produced significantly less output in response to a frog’s thump. This pattern of geophone outputs in response to the seismic thump associated with the frog’s call is con-

Figure 3. a. A single chirp vocalization recorded with microphone (upper trace) and its associated thump (lower trace) recorded with the geophone located 1 m from the calling male. b. Chirp velocity spectrum, average of 256 samples, smoothed with a Hanning window of width 30 Hz. c. Thump velocity spectrum, average of 256 samples, smoothed with a Hanning window of width 3 Hz. d. Histogram showing the distribution of best vibratory frequencies for 37 afferent fibers recorded from the eighth nerve of the white-lipped frog, Leptodactylus albilabris. The fibers fell into two distinct groups: a low-frequency population exhibiting extreme sensitivity to substrate-borne vibrations, and a second, higher-frequency, less-sensitive group. (From Lewis and Narins 1985. Reprinted with permission. © 1985 American Association for the Advancement of Science.)
sistent with the production of surface (Rayleigh) waves, known to subserve prey detection in desert scorpions (Brownell 1977, Brownell and Farley 1979), as well as in various other invertebrates (Markl 1983).

Production of substrate vibrations

To transmit biologically significant information among individuals, some species have exploited the properties of surface waves. Animals may generate these waves by applying an impulsive or periodic force to the medium surrounding them, after which the propagation and reception depends on the composition of the substrate and the background noise in the channel.

Males of *L. albilabris* produce two distinct vocalizations: the species’ advertisement call (chirps) and the species’ aggressive call (chuckles), emitted during male-male acoustic interactions (Lewis and Narins 1985, Lopez et al. 1988). Often found partially embedded in water-saturated substrates, males call with only the anterior half of their body above ground level. As the vocal sac explosively expands during a chirp vocalization, for example, it strikes the substrate with enough force to generate a surface wave, which propagates from the calling male in all directions (Figure 3a).

Detection of earth-borne signals

How does a frog detect extremely small motions of the substrate? Anatomical and physiological studies have shown that the vibration sensitivity of terrestrial frogs and toads resides principally in the sacculus of their inner ear (Koyama et al. 1982, Lewis et al. 1982). The sacculus is an otolithic organ containing a membrane sac filled with a slurry of dense calcium carbonate crystals. The 3000 sensory hair cells in the sacculus of the North American bullfrog (*Rana catesbeiana*), for example, are concentrated in a macula with their stereocilia in contact with the overlying otoconial mass, which can be 20 mg in an adult frog (Lewis and Lombard 1988). When the animal undergoes an acceleration, the vibrations reach the sacculus, where they are believed to set up a traveling wave, much like the vibration pattern known to occur on the basilar membrane in the mammalian cochlea (Lewis and Lombard 1988). The traveling wave results in the shearing of the stereocilia of the sensory hair cells in the saccular macula, caused by the differential motion between the sensory epithelium and the otoconial mass. This motion leads directly to a modulation of the resting discharge rate in the afferent fibers innervating the saccular hair cells.

The pathway by which the sacculus receives vibratory input has long been the subject of debate (Hetherington 1985, Lombard and Straughan 1974, Paton 1971). Recently, Hetherington (1988) has shed light on this question by directly testing the effect of the opercularis system on the transmission of low-frequency vibratory stimuli to the inner ear of the bullfrog (Figure 4a). This system in amphibians includes the opercular muscle, which connects the pectoral girdle with the operculum, a movable, cartilaginous element in the oval window of the otic capsule (Figure 4b). Hetherington found that removal of the opercular muscle reduced electrical (microphonic) responses in the inner ear to vertical vibrations, especially for low frequencies. Moreover, the decrease in the response to vertical vibrations was greater than for longitudinal or transverse accelerations of the same magnitude. The opercularis system of the bullfrog thus appears to be specialized for transmitting vertical substrate motions to the inner ear.

The neural basis for seismic signal detection

To investigate the neural basis of this remarkable behavior, in collaboration with E. R. Lewis at the University of California at Berkeley I have studied the responses of single fibers in the eighth (acoustic-vestibular) cranial nerve to whole-body vibrations in *L. albilabris*. A male frog is anesthetized and placed on a platform that can be sinusoidally vibrated over a wide range of frequencies and amplitudes. To properly isolate the animal from ambient microseismic vibrations, it is necessary to enclose the entire recording apparatus and the animal in a specially designed vibration-damped room, in which the vibration noise floor is reduced to at least an order of magnitude lower than any stimulus being applied. In the case of the white-lipped frog, it was necessary to obtain a vibration noise floor of 0.0001 cm/s², enabling accurate measurements of accelerations down to 0.001 cm/s².

Single saccular fibers in the eighth cranial nerve were impaled with KCl-filled glass micropipettes to record responses to whole-body vibrations. Vibratory-sensitive fibers show a characteristic tuned response; that is, each fiber responds most vigorously (highest discharge rate) to a best vibratory frequency (BVF), analogous to the best excitatory frequency of auditory fibers. We found two populations of fibers that responded selec-
200 and 300 Hz (Figure 3d). The most sensitive fibers in this species respond to peak whole-body accelerations on the order of 0.001 cm/s² (Narins and Lewis 1984). This represents a seismic sensitivity of approximately an order of magnitude greater than saccular fibers in the North American bullfrog, *Rana catesbeiana* (Koyama et al. 1982) and four orders of magnitude greater than has been reported for mammalian inner ear organs. The response of a representative vibration-sensitive fiber from the white-lipped frog is shown in Figure 5.

**Communication signals**

Other vertebrates for which seismic communication has been implicated are kangaroo rats, *Dipodomys* (Randall 1989, Randall and Stevens 1987); kangaroos, *Thylagale* (Gregory et al. 1986); and mole rats, *Spalax* (Heth et al. 1987, Rado et al. 1987) and *Georychus*. Surface foot drumming by kangaroo rats produces clear audible as well as seismic cues. Whether these desert animals use substrate vibrations for intraspecific communication, or if they are instead unavoidable consequences of acoustic signaling by drumming, remains to be experimentally tested.

The available evidence for seismic communication in a wallaby known as the Tasmanian pademelon is anatomical. A group of lamellated corpuscles, similar to the Pacinian corpuscles of eutherian mammals, has been identified in the leg joints of this animal. These mechanoreceptors are thought to function in the detection of ground-borne vibrations.

The most convincing evidence for seismic signaling in interspecific communication by a higher vertebrate comes from experimental work with mole rats (order Rodentia, families Spalacidae and Bathyergidae). These subterranean rodents produce temporally complex thumps either by head drumming (*Spalax*) or foot drumming (*Georychus*). Several species show clear cochlear adaptations for the reception of low-frequency stimuli, and individual mole rats respond to conspecific thumps by initiating a thump-

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1 M. Narins et al., 1990, unpublished data.

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![Figure 5](https://example.com/figure5.png) Phase histograms showing response of a single seismic afferent fiber in the eighth nerve of *Leptodactyulus albilabis* to a series of vibratory stimuli at the fiber’s best vibratory frequency of 100 Hz for decreasing peak accelerations: a, 0.005 cm/s²; b, 0.0028 cm/s²; and c, 0.0016 cm/s². Vertical axis is the number of spikes in a 3.6° phase bin; horizontal axis is the phase of the stimulus sinusoid. Histograms represent averages of 35–45 s of spike data. Note clear sinusoidal modulation of discharge rate in response to even the smallest acceleration tested.

1. E. R. Lewis et al., 1990, unpublished data.

University of California, Berkeley.
males in the proximity of other calling males react quite differently to finger tapping on the substrate and continue to vocally interact with each other.

Thus the extreme seismic sensitivity observed in the behavior of isolated males in nature (as well as in the laboratory) appears to change under chorus conditions. The exact mechanism underlying this switching is not yet understood, but it is likely to be related to the concomitant detection of vocalizing conspecific males, because the frequency content of the frog's thump and that of light finger tapping are almost identical.

What is the selective advantage of producing both an airborne and a substrate-borne component of an advertisement signal? Rayleigh waves in the Puerto Rican soil propagate at approximately 100 meters per second, roughly one-third the speed of sound in air. If the frog were able to separate the airborne and substrate-borne components of a neighbor’s call and integrate them in its central nervous system, he could theoretically use the time of arrival difference between the two call components as a measure of the distance to his neighbor. This information could be useful in setting up and maintaining spacing patterns in the chorus (Brush and Narins 1989).

A second reason for the production of the two call modalities could be related to the task an animal confronts when forced to communicate biologically significant information in the midst of high ambient noise levels. For the white-lipped frog, the mean background noise level within a nocturnal chorus due to the cacophony of conspecific and heterospecific frog calls and insect sounds in the Luquillo Mountains in eastern Puerto Rico is typically 80–90 dB sound pressure level peak (Narins 1982).

Three strategies come to mind that would enable an individual calling male to overcome this formidable acoustic barrier. First, the frog could use a private portion of the frequency spectrum and thus avoid acoustic interference by spectral separation. This possibility assumes that the frog possesses the neural hardware necessary to filter out a conspecific call from those of closely related species in its environment. Also implicit in the spectral-separation hypothesis is the assumption that individuals are able to adjust the frequency of their calls to avoid interference with conspecifics. Available evidence suggests that spectral filtering alone is insufficient to account for the species specificity of the call of most amphibians (Narins and Zelick 1988). Moreover, at least in the case of the white-lipped frog, frequency adjustments observed are in the wrong direction for acoustic avoidance (Lopez et al. 1988).

Another option might be for an individual to call during times when other species are inactive, thus avoiding overlap by partitioning the acoustic environment. Such time-sharing has been shown to take place on a diel scale for an assemblage of neotropical frogs (Drewry and Rand 1983) and on a second, or even millisecond, time scale for intraspecific interactions (Littlejohn and Martin 1969, Zelick and Narins 1982).

A third, more radical, alternative is for the frog to produce, concomitant with the call, a seismic surface wave that propagates in the relatively quiet substrate channel. Measurement of the background noise in the soil shows that microseismic noise levels at the earth’s surface are extremely low, typically on the order of 0.0005 cm/s² per Hz½ in the absence of machinery, traffic, and high winds (Frantii et al. 1962). Thus it is possible that some ground-dwelling amphibians develop paired acoustic and seismic signals, which are transmitted in separate but parallel channels. This strategy would provide redundancy to better communicate when high-level background noise obscures the acoustic channel. In the Caribbean National Forest of eastern Puerto Rico, it appears that the white-lipped frog uses the substrate as a communication channel.

Conclusions
Seismic communication offers many advantages for terrestrial animals. It can take place day or night and carry information to nearby conspecifics without danger of detection by more distant predators. Many terrestrial animals, including the white-lipped frog, _L. albilabris_, are sensitive to low-level substrate vibrations. A male white-lipped frog generates a seismic wave, from its vocal sac expanding explosively, when it produces a chirp vocalization. Frogs of this species sense ground motion with an organ of the inner ear. We have discovered two populations of nerve fibers that respond to whole-body vibrations. The most sensitive fibers respond to vibrational frequencies of the peak energy in the frog seismic thumps. We suggest that frog seismic communication could be used to set up spacing patterns in the chorus and to identify the relevant acoustic chirp within the cacophony of frog calls and insect sound. The white-lipped frog is the first vertebrate for which strong anatomical, neurophysiological, and behavioral evidence indicates seismic communication within a species. There is also some evidence for seismic communication in kangaroo rats, kangaroos, and mole rats.

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